NEW RECORDS AND REDESCRIPTIONS OF THECATE HYDROIDS FROM SOUTHERN AUSTRALIA

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Five species of hydroids formerly thought to be rare are redescribed and their ecology discussed. These are a hydroid doubtfully assigned to *Clytia hemisphaerica* Linnaeus, 1767, *Silicularia undulata* (Mulder & Trebilcock, 1914), *Thyroscyphus macrocytharus* (Lamouroux, 1824), *Clytia paulensis* (Vanhöffen, 1910), and the hydroid and medusa stages of *Phialella quadrata* (Forbes, 1848). Two other species, *Lafoeina amirantensis* (Millard & Bouillon, 1973) and *Aglaophenia postdentata* Billard, 1913 are new records for Australia.

COLLECTIONS (mostly by the author) along the southern Australian coastline have yielded five species of hydroids formerly thought to be rare in the region, and two new records for Australia.

Lafoeina amirantensis (Millard & Bouillon, 1973), and *Aglaophenia postdentata* Billard, 1913 are new records for Australia. *Lafoeina amirantensis* is recorded from Bass Strait in the south-east, and *A. postdentata* from the south-west of the continent. The hydroid of *Phialella quadrata* (Forbes, 1848), previously recorded as *Lovenella briggsi* Mulder & Trebilcock, 1915, is redescribed together with two stages in the development of the medusa. *Clytia ?hemisphaerica* Linnaeus, 1767, and *Silicularia undulata* (Mulder & Trebilcock, 1914) were previously recorded from few Australian localities; these species are now known to be widespread across the southern continent. Although it was one of the earliest described hydroids from Australia, *Thyroscyphus macrocytharus* (Lamouroux, 1824) has been misidentified in the past: the species is here redescribed.

Material lodged in the Museum of Victoria is denoted by the prefix NMV.

Family Campanulinidae Hincks, 1868

Genus Lafoeina M. Sars, 1874

Calder (1991) discussed the systematic status of the closely related genera *Lafoeina* and *Egmundella* and because of their obscure family affiliations and the lack of information on their reproductive structures, excluded them from the Campanulinidae. He distinguished *Lafoeina* from *Egmundella* chiefly on the basis of its cylindrical and sessile or nearly sessile hydrotheca, the lack of a basal perisarcal shelf, and its oval nematophores. In *Egmundella*, hydrothecae are conical and pedicellate, a perisarcal shelf is present and nematophores are tubular to clavate. He referred material from Bermuda, corresponding to *Egmundella amirantensis* Millard & Bouillon, 1973 from the Indian Ocean, to *Lafoeina*.

Specimens from Bass Strait possess clavate nematothecae which agree perfectly with Millard & Bouillon's description of *Egmundella amirantensis* but agree less well with Calder's figure (fig. 3, p. 10) of his Bermuda specimens. The hydranths of the Bass Strait specimens have a distinct base which rests upon the narrow floor of the hydrotheca but the perisarcal shelf is absent. Following Calder, the Bass Strait material is here referred to *Lafoeina*. However, until the relationships of *Lafaoeina* and *Egmundella* are better known, *Lafoeina* is provisionally retained in the Campanulinidae.

Lafoeina amirantensis (Millard & Bouillon, 1973)

Fig. 1A

Lafoeina amirantensis (Millard & Bouillon).—Calder, 1991: 10, fig. 3.

Egmundella amirantensis Millard & Bouillon, 1973: 40, fig. 5A–D.—Millard, 1975: 133, fig. 43G.—Garcia-Corrales, Arcas & De Diego, 1979: 27, fig. 14.—Roca, 1986: 9.—Gibbons & Ryland, 1989: 389, fig. 7.—Ramil & Vervoort, 1992: 22, fig. 2a–d.

Material and record. NMV F51790. Mieroslide. Ninety Mile Beach, Bass Strait, 38°13'S,147°13'E, 1 km offshore from Delray Beach, on the stems of *Tubularia exxonia* Watson, 1978, 10 m, N. W. Watson, 20/4/91.

Description. Hydrorhiza reptant, hydrothecae variable in length, arising directly from the hydrorhiza on very short but distinct pedicel, a faint constriction of the perisarc separating hydrotheca from pedicel; hydrotheca narrowest at base, body cylindrical or widening slightly to margin, often narrowing just below origin of operculum. Oper-

culum consisting of approximately 10 long, sharply pointed segments, not clearly demarcated from margin. Hydranth with 10–14 tentacles, capable of considerable extension and deep withdrawal into the hydrotheca; base of hydranth seated on a slight thickening of the perisarc immediately above the pedicel.

Nematothecae borne on the hydrorhiza, one between every three or four hydrothecae, clavate, maximum width about two-thirds the distance up

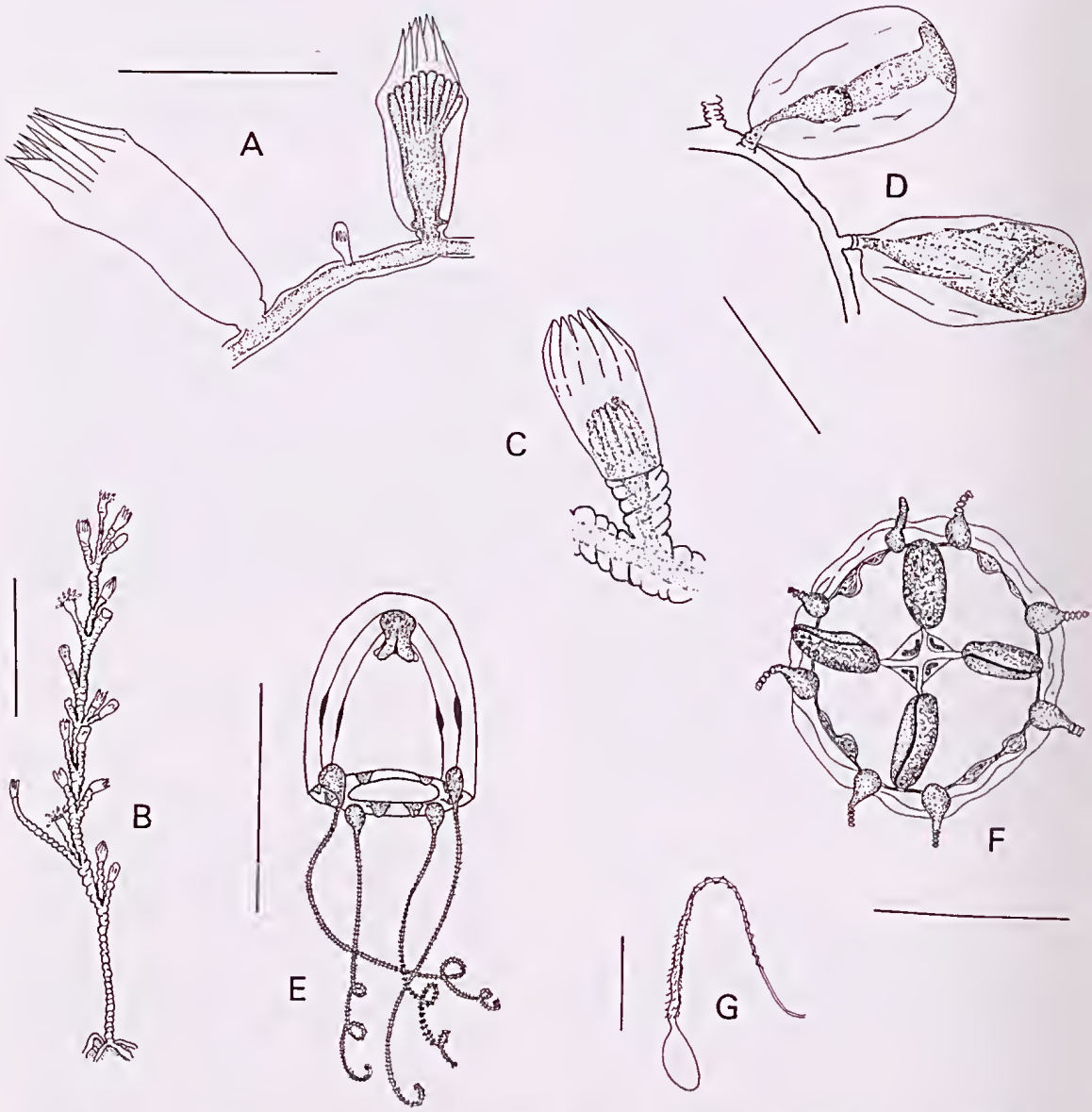

Fig. 1. A–F. A, *Lafoeina amirantensis*, part of colony from Bass Strait with hydrothecae and nematotheca. B–G, *Phialella quadrata*, mature stem from Western Port, Victoria. C, hydrotheca showing opercular segments. D, immature gonothecae. E, newly released medusa from colony from Western Port, living specimen. F, eight-tentacle stage medusa from Port Kembla, New South Wales, preserved material. G, discharged microbasic mastigophore from newly released medusa. Bar scales: A, C, D, 0.2 mm; B, E, 1 mm; F, 3 mm; G, 10 μm.

from base, body narrowing to a small circular orifice; several clongate nematocysts clustered inside.

Perisarc of colony very delicate and almost transparent, thinning distally on hydrotheca.

Measurements (mm). Width of hydrorhiza 0.05, length of hydrotheca from base to origin of operculum 0.14–0.27, width at margin 0.10–0.15, length of nematotheca 0.05–0.07, maximum width 0.02.

Remarks. The colonies were abundant on stems of *Tubularia exxonia* growing on a buoy-line. The rope had been immersed for a period of eight weeks, during which time it was heavily colonised by *T. exxonia*. *Lafoeina amirantensis* is an opportunistic shallow water epizooite of other hydroids (Millard & Bouillon 1973; Garcia-Corrales et al. 1979; Calder 1991; Ramil & Vervoort 1992) and is an occasional epiphyte of weed (Millard & Bouillon 1973). The record of Gibbons & Ryland (1989) from Fiji is also from a tubularian hydroid.

This is the first record of *Lafoeina* from Australia.

Family **Phialellidae** Russell, 1953

Genus **Phialella** Browne, 1902

The genus *Phialella* is known from five species (Boero 1987). These are: *Phialella quadrata* (Forbes, 1848), *Phialella hyalina* (von Lendenfeld, 1885), *Phialella falklandica* Browne, 1902, *Phialella fragilis* Uchida, 1938, and *Phialella zappai* Boero, 1987. *Phialella quadrata* is the most widely distributed of these species, being recorded from the Indo-Pacific, Japan, New Zealand, Chile and north-western Europe (Kramp 1968).

Phialella quadrata (Forbes, 1848)

Fig. 1B–G

Mulder & Trebilcock (1915) described the hydroid *Lovenella briggsi* from south-eastern Australia; it was next recorded as *Phialella briggsi* (Mulder & Trebilcock, 1915) from *Amphibolis* seagrasses by Watson (1992). Further collecting shows it to be a very common species in many southern Australian habitats.

I have compared microslide specimens of Mulder & Trebilcock's *L. briggsi* in the Museum of Victoria collection (NMV F57997, four microslides labelled 'Corio Bay'; F57998, three microslides, labelled Torquay) with fresh material and have found no features that distinguish it from *Phiallela quadrata*. I therefore refer *Lovenella briggsi* to *Phialella quadrata* (Forbes, 1848).

From records of the medusa of *P. quadrata* from New Zealand (= *Eucope annulata* von Lendenfeld, 1885, see Ralph 1957), Southcott (1982) presumed its range extended to southern Australia. Von Lendenfeld (1885b) also described a second medusa as *Eucope hyalina* von Lendenfeld, 1885, from Port Jackson, New South Wales. Kramp (1953) regarded *E. hyalina* as a distinct species but later doubted its validity (Kramp 1968, p. 84). I have examined the type material of *E. hyalina* held in the Australian Museum: it consists of fluid preserved material and one microslide preparation, mounted in Canada Balsam and labelled 'Type Y182'. The specimens in fluid have decomposed beyond recognition; the microslide consists of three reasonably well preserved medusae, two of which are arranged in lateral view and the other in transverse aspect. The medusae have eight tentacles and eight adradial vesicles. Only one statolith is visible near each adradial bulb, not three, as stated by von Lendenfeld. Medusae collected by the author from New South Wales near von Lendenfeld's type locality are clearly referrable to *P. quadrata* as described and figured by Kramp (1968), Russell (1953) and Boero (1987).

Kramp (1968) considered the medusa of *P. quadrata* to be conspecific with *P. fragilis* (Uchida, 1938) from Japan. Boero (1987) however, regarded them as distinct although very closely related species, the two main points of difference being the triangular tentacle bulbs of *P. fragilis* (those of *P. quadrata* being globular), the absence of nematocysts from the exumbrella, the quadrate manubrium and the absence of interradial tentacle bulbs on newly released *P. fragilis*. Manubria of very young medusae of *P. quadrata* examined in the present study were seen to rapidly change from quadrate to cruciform shape, depending upon the state of extension of the tentacles. At the same time, the tentacle bulbs changed shape from globular to triangular. Other than the absence of rudimentary interradial tentacle bulbs from *P. fragilis*, the hydroid and medusa phases of the two species are identical. However, until the taxonomic significance of the rudimentary interradial tentacle bulb is better known, *P. fragilis* and *P. quadrata* should be regarded as separate species.

The first three growth stages of the medusa of *P. quadrata* have been recorded in the present study. Liberation of large numbers of the earliest (four-tentacle) stage medusae from late summer colonies of *P. quadrata* from Western Port, Victoria, was observed in the laboratory; the eight-tentacle stage was found in abundance in summer plankton hauls in the harbour of Port Kembla, New South Wales and several medusae at the 16-

tentacle stage were collected in a late autumn (May) plankton haul from eastern Bass Strait.

The genus *Phialella* as now envisaged comprises *P. quadrata*, *P. fragilis*, *P. falklandica* and *P. zappai*.

The hydroid of *P. quadrata* and the two early medusa stages from Australia are described.

Thaumantantias quadrata Forbes, 1848: 43, pl. 9, fig. 2.
Eucope annulata von Lendenfeld, 1885a: 602, pl. 28, figs 52–57.
Eucope hyalina von Lendenfeld, 1885b: 920, pl. 42, figs 16–18.
Lovenella briggsi Mulder & Trebilcock, 1915: 57, pl. 9, figs 3–3f.
Phialella quadrata (Forbes).—Ralph, 1957: 848, fig. 8g–i.—Kramp, 1968: 84, fig. 226.—Southcott, 1982: 135, fig. 4.26d.

Material and records. NMV F51791. Fertile colony, with newly released medusae, preserved material, Western Port, Victoria, on the green alga *Caulerpa cactoides* 3 m, J. E. Watson, 2/1/92. NMV F51792. Medusa from plankton haul, subsurface, Port Kembla Harbour, New South Wales, J. E. Watson, 25/9/91.

Description of hydroid. Colonies both stolonal and erect. Hydrorhiza tubular, loosely adherent to the substrate. Stems small, unfascicled, corrugated throughout, rarely with smooth patches, perisarc thicker proximally, becoming thinner distally.

Proximal stem region unbranched, branching thereafter pseudo-sympodial, but often two to four hydrothecae given off from the same stem internode. Pedicel of hydrotheca corrugated, perisarc thinning distally and widening gradually to merge into base of the hydrotheca.

Hydrotheca almost cylindrical distally, widening slightly to margin, a transverse to oblique diaphragm near the base and above it a circle of desmocytes at the point of attachment of the hydranth. Young hydrothecae with a conical operculum of about eight very delicate wedge-shaped segments with blunt apex, the opercular flaps opening to form the margin. Hydranth with about 16 long moniliform tentacles armed with the same nematocysts as in the medusa (see below).

Gonothecae borne singly on hydrorhiza or hydrocauli, pedicel short, with one or two annulations, variable in shape from almost cylindrical to elongate top-shaped, widening distally, summit truncated, perisarc thin and smooth, containing one medusa and sometimes one medusa bud. The distal perisarc ruptures at release of the medusa leaving a loose sheath of tissue protruding.

Measurements (mm). Height of stem 5, proximal width 0.06–0.07, hydrothecal pedicel 0.13–0.3, proximal width 0.06–0.08, width at diaphragm 0.06–0.07, width at margin 0.08–0.10, distance from diaphragm to end of apertural flaps 0.15–0.21, height of gonothecae including pedicel 0.62–0.80, maximum width 0.35–0.50.

Description of medusa. Medusa at liberation dome-shaped, jelly thick, deeper than wide, velum broad, with four perradial tentacles with oval to triangular bulbs, tentacles long, moniliform when extended, with clusters of nematocysts. Four thin radial canals each with a rudimentary gonad in the distal third; four undeveloped interradial tentacle bulbs and eight adradial statocysts each with two statoliths on the ring canal. Manubrium saccate, mouth quadrate with four short lips and a few nematocysts. Four dark markings in the interradial position at base of the stomach. No umbilical canal and no exumbrellar nematocysts. Tentacular nematocysts microbasic mastigophores, shaft thick, with long spines, thread thin, spinous.

Preserved specimens at the eight-tentacle stage with elongate stomach and manubrium with slightly fluted lips; four characteristic interradial brown-black spots at the junction of peduncle with exumbrella. At this stage the gonads are hollow canoe-shaped structures occupying the distal third of the radial canals; some contain ripe ova.

Measurements. Four-tentacle stage medusa—height 1.5 mm, width 0.8 mm, length of manubrium 0.3 mm, capsule of tentacular nematocysts 7–9 μm × 4–7 μm, shaft to 15 μm, length of thread 100 μm. Eight-tentacle stage medusa—height, 2.8–3 mm.

Colour. Colonies white to colourless. Medusa at liberation transparent, stomach and perradial tentacle bulbs yellow to pale brown. Older medusa (preserved material) clear, gonads white to creamy pink.

Remarks. The hydrothecal diaphragm of the hydroid is usually transverse, but in some hydrothecae it is oblique. The diaphragm forms the junction between the pedicel and hydrotheca and is a point of weakness at which hydrothecae often break away. Distal stolonisation as described for *P. fragilis* by Boero (1987) is very common and appears to be a result of environmental stress to the colony.

Newly released medusae were sluggish during the 24 h of observation in the laboratory, spending much time motionless on the bottom of the vessel, slow exploration by the tentacles being interrupted by occasional feeble swimming movements. No scattered nematocysts were seen on the exumbrella of the medusa as reported for European *P. quadrata* by Russell (1953).

Eight-tentacle stage medusae were among a summer plankton haul from an industrial harbour on the central coast of New South Wales. The hydroid was not found in the harbour. Sixteen-

tentacle stage medusae were captured in a plankton haul by the author in eastern Bass Strait in May, 1992.

The hydroid of *P. quadrata* is very common in summer in southern Australia (Watson 1992), growing on a wide variety of algae, seagrasses and invertebrate substrates in ocean and bays to depths of at least 25 m. The only previous record of the medusa is from Sydney, New South Wales as *Eucope hyalina* (von Lendenfeld, 1885).

Family Campanulariidae Hincks, 1868

Genus Clytia Lamouroux, 1812

Clytia ?hemisphaerica (Linnaeus, 1767)

Fig. 2A–E

Medusa hemisphaerica Linnaeus, 1767: 1098.
Laomedea gracilis M. Sars, 1851: 138.
Clytia gracilis (M. Sars).—Steehow, 1924: 69; 1925: 212.—Cornelius & Östman, 1986: 165.—Calder, 1991: 54.
Campanularia johnstoni Alder.—Bale, 1924: 232.—Ralph, 1957: 820, 823, figs 1h–u, 2, 3a–f.—Pennyeuik, 1959: 170.
Campanularia serrulata Bale, 1888: 757, pl. 12, fig. 4.—Steehow, 1919: 46, fig. M.—Calder, 1991: 56.
Phialidium hemisphaericum (Linnaeus). Russell, 1953: 285–294, pl. 16, fig. 1, pl. 17, fig. 6, text-figs 172–179.—Kramp, 1965: 60; 1968: 76, 150–152, fig. 201.

For world synonymy see Cornelius 1982: 73.

Material and records. NMV F51793. Hydroid eolony, preserved material, Ninety Mile Beaeh, Bass Strait, Vietoria, 6 m, on buoy line 1 km offshore from Delray Beach, R. C. Langley, 20/5/1992. NMV F51801. Medusae, preserved material, lower Port Phillip Bay, on red alga, 10 m, J. E. Watson, 17/7/92.

Description of hydroid. Hydrorhiza tubular, 0.05–0.10 mm wide, loosely reptant on substrate.

Stems simple, slender and fragile, sometimes branched once, with up to 15 proximal and 8–10 distal annulations, remainder of stem smooth or with groups of two to three annulations. Hydrotheca conical, expanding evenly from base to margin, circular to subcircular in cross section, basal chamber below diaphragm contiguous with hydrotheca, perisarc delicate, thinning towards margin. Margin with 8–10 evenly spaced teeth, cusps variable in shape from sharply pointed to blunt, with wide incisions between. Hydranth with 12–16 tentacles.

Gonothecae borne on the hydrorhiza on a slightly twisted pedicel, barrel-shaped, walls smooth or sometimes slightly undulated, distally truncate, a constriction just below the margin, summit concave. Gonophore with one to three developing medusa buds, medusa released by rupture of the perisarc.

Measurements of hydroid (mm). Height of stems to 5, diameter of stems 0.07–0.10, length of hydrotheca 0.35–0.75, diameter of basal chamber 0.13–0.17, diameter at margin 0.27–0.55, height of marginal teeth 0.06–0.07, width of incision between teeth 0.08–0.09, length of gonotheca 0.55–1.00, width 0.35–0.50.

Description of medusa. Release of medusae was observed in the laboratory. At liberation the medusa is almost hemispherical, jelly relatively thick and velum broad; scattered nematocysts on the exumbrella or in a band encircling the middle of the exumbrella. Stomach short, manubrium broad, with four poorly defined lips armed with nematocysts. Radial canals narrow, rudimentary gonads situated in the middle of each canal. Ring canal narrow with four perradial tentacles arising from oval marginal bulbs, one rudimentary tentacle bulb between the perradials and eight adradial statocysts each with one statolith. Tentacles hollow, long and extensile, richly armed with nematocysts. Nematocysts on exumbrella and tentacles microbasic mastigophores, capsule bean-shaped, spinous, thread moderately thick and very long.

Measurements of medusa. Exumbrella 0.66 mm high, width 0.85 mm, capsule of nematoeyst 7×2 μm, shaft 6 μm, minimum length of thread 90 μm.

Colour. Colonies colourless to translucent white. Medusa colourless, tentacle bulbs and stomach pale yellow.

Remarks—Hydroid. The dentition of the hydrothecal margin of the present material is quite variable, most hydrothecae in a colony having blunt teeth, sometimes with truncated cusps; some cusps are however, sharply pointed, and more rarely, slightly skewed. Hydrocauli are seldom branched, but when so, branching is by means of a secondary pedicel arising from the proximal section of the primary stem.

Clytia hemisphaerica (as *Campanularia johnstoni* Alder, 1856) has been recorded from subtropical Queensland (Pennycuik 1959) and the closely related *Clytia gracilis* (M. Sars, 1851) was recorded from Western Australia by Stechow (1924, 1925). I have examined a microslide specimen (Canada Balsam mounted) of *Campanularia serrulata* prepared by W. M. Bale, in the collection of the Museum of Victoria (NMV F58758), labelled 'Port Jackson 1888' and probably part of Bale's type series (Stranks 1993). Cornelius (1982) and Calder (1991) considered *C. serrulata* to be a synonym of *Clytia hemisphaerica*. Bale's specimen,

attached to a fragment of seagrass, consists of numerous proximally and distally annulated stems. Most are simple but several are forked one or more times. The hydrothecae have bluntly pointed teeth separated by deep saddle-shaped incisions similar to the present specimens: no skewing of the teeth is evident.

Many authors [e.g. Cornelius (1982, 1992), Calder (1991)], have attempted to distinguish between *Clytia hemisphaerica* and *Clytia gracilis* on morphology of the hydrothecae. Calder (1991) considered that the usually skewed marginal teeth and spirally ribbed gonotheca of *C. hemisphaerica* were sufficient to distinguish it from the rounded cusps and smooth gonothecal walls of *C. gracilis*. Conversely, Cornelius (1982), figured a hydrotheca of *C. hemisphaerica* with distinctly skewed teeth but later, (1992), described *C. gracilis* as having a hydrotheca with cusps pointing to one side.

The small, delicate hydrothecae and smooth to

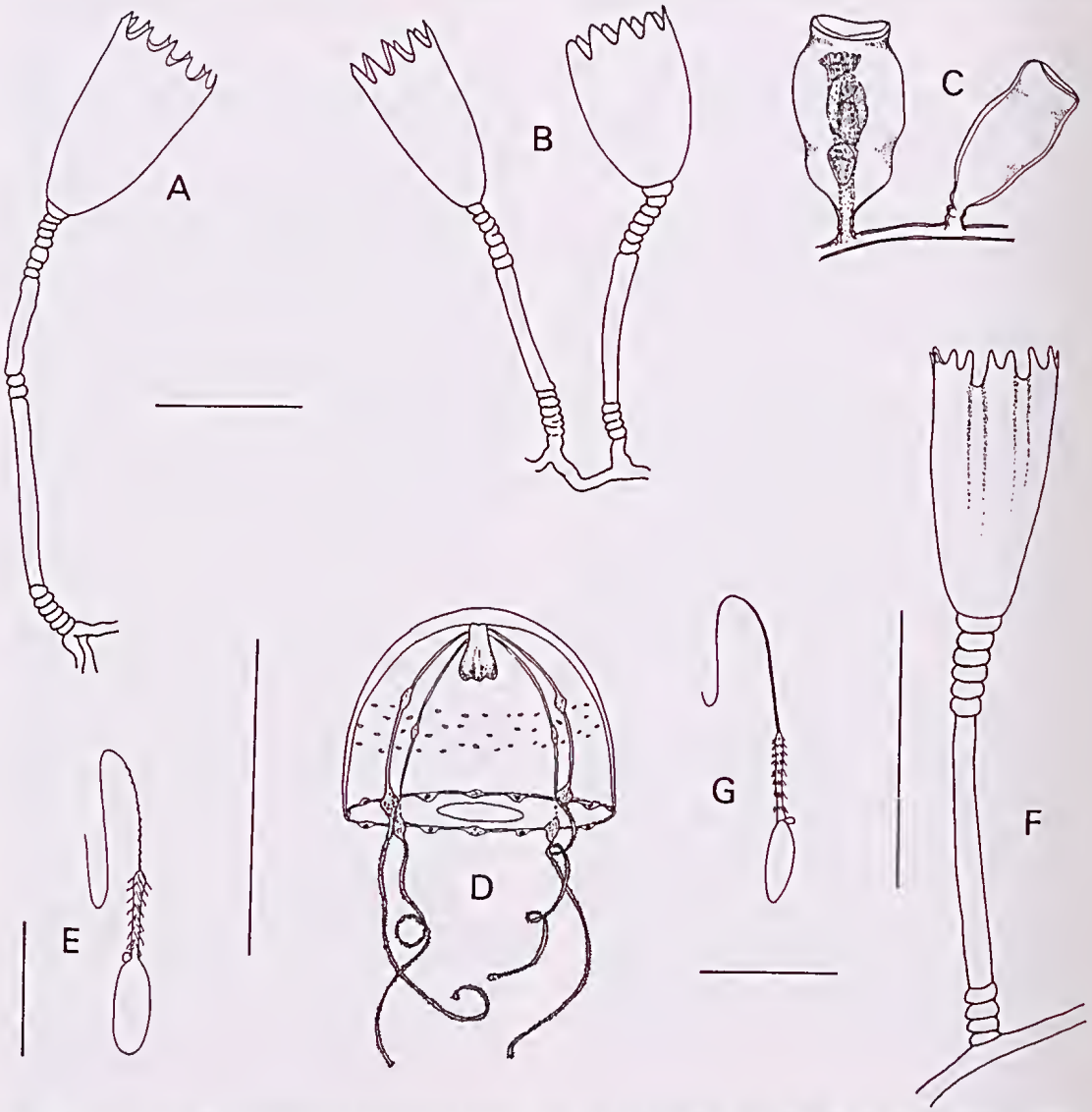

Fig. 2. A–G, *Clytia hemisphaerica* from Port Phillip Bay. A, B, hydrothecae with rounded to pointed cusps. C, gonothecae. D, newly released medusa, living specimen. E, discharged microbasic mastigophore from medusa. F, G, *Clytia paulensis* from Port Phillip Bay, Victoria. F, hydrotheca. G, discharged microbasic mastigophore from hydranth. Bar scales: A–C, E, 0.5 mm; D, 1 mm; E, 10 μm.

faintly undulated gonothecae place the present specimens near *C. gracilis*; on the other hand, other characters such as the sometimes skewed teeth place it within the range of *C. hemisphaerica*.

In this state of taxonomic confusion it is impossible on colony morphology alone to assign the present material or Bale's *C. serrulata* to either *C. hemisphaerica* or *C. gracilis*. Cornelius & Östman (1986) and Östman (1987) were able to distinguish *C. hemisphaerica* from *C. gracilis* on the fine structure of the cnidome. Thus until examination of the cnidome of fresh material is carried out, the south-eastern Australian material is doubtfully assigned to *C. hemisphaerica*.

The hydroid is highly opportunistic, occurring on many invertebrate and red algal substrates and man-made structures. Colonies on natural substrates are usually small, comprising a few to tens of hydrocauli. In contrast, those on hard surfaces are often very prolific: for example, up to 50 hydrocauli per cm^2, and twice that number of gonothecae were counted on an experimental panel deployed for six weeks in Bass Strait (J. E. Watson, unpubl.). The hydroid is also abundant on drifting stems of the coastal seagrass *Heterozostera tasmanica* (Martens ex Aschers.) den Hartog, and in this respect, resembles the pelagic colonies mentioned by Cornelius (1982).

Australian records are from the intertidal zone to 33 m deep. Distribution is from Western Australia to southern Queensland on algal substrates and the seagrasses *Halophila spinulosa* and *Amphibolis antarctica*, the alcyonarian *Telesto smithi* and on other hydroids (Stechow 1925; Pennycuik 1959; Watson 1992 and unpubl.).

Remarks—Medusa. The medusa of *C. hemisphaerica* has previously been recorded once, without description, from the Tasman Sea off the Australian continental shelf (Kramp 1965).

In a study of the life cycle of *Clytia edwardsi*, Kubota (1978) showed that the exumbrella nematocysts were arranged in a band in newly released medusae and were gradually shed with increasing maturity. He suspected, and Cornelius (1982) concurred, that *C. edwardsi* is conspecific with *C. hemisphaerica*. Kubota also reported three kinds of nematocysts in the medusa—two kinds of macrobasic mastigophores on the bell and lips and atrichous isorhizas in the tentacles. The resemblance between the three kinds of nematocysts (see Kubota 1978) may be the reason for their not being detected in the present material. Several medusae among the present specimens had five or six radial canals, and the bell was seen to frequently contract into the characteristically quadrate shape described by Russell (1953).

Newly released medusae were sluggish, remaining contracted for long periods on the bottom of the vessel. At the same time however, the manubria were very active, exploring the inside of the bell.

Clytia paulensis (Vanhöffen, 1910)

Fig. 2F, G

Campanularia paulensis Vanhöffen, 1910: 298, fig. 19.
Clytia paulensis (Vanhöffen).—Stechow, 1919: 45, 155; 1923: 110, fig. N; 1925: 211.—Millard, 1975: 221, fig. 73a–d.—Cornelius, 1982: 88–91, fig. 14.

Material and record. NMV F51794 microslide Port Phillip Bay, on *Obelia australis* von Lendenfeld, 1885, 10 m, J. E. Watson 29/2/92.

Description. Hydrorhiza tubular, running up the stems and along the branches of the host. Pedicels given off at regular intervals, slender, tubular, perisarc smooth and glassy with 7–12 proximal and 4–9 distal deep annulations. Hydrotheca deep, conical, walls straight, expanding to margin. Margin with six pairs of bidentate teeth, each tooth with a slightly blunt apex, teeth sometimes inclined inwards, a shallow saddle separating each pair of cusps and a deep U-shaped incision between the pairs, often an indistinct ridge passing from the sides of the incision down into the hydrotheca. Hydranth with 12–16 tentacles held out stiffly in an amphicoronate arrangement from the hydrotheca. Tentacular nematocysts microbasic mastigophores, capsule elongate, shaft spinous, thread long.

Material sterile.

Measurements. Pedicels 0.65–0.82 mm long, diameter, 0.04–0.05 mm, length of hydrotheca, diaphragm to margin, 0.47–0.5 mm, width at margin 0.18–0.21 mm, depth of tooth from cusp to base, 0.04 mm. Capsule of tentacular nematocysts 5×1.5–$2\ \mu m$.

Remarks. The only previous record of *Clytia paulensis* from Australia is that of Stechow (1924, 1925) who briefly described but did not figure a specimen from Shark Bay, Western Australia. The present specimens are larger than measurements given by Stechow (hydrotheca, 0.3 mm, marginal width, 0.13 mm) but fall within the range given by Millard (1975) for specimens from southern Africa.

Some stems of the present material are branched by means of a secondary pedicel given off below the distal annulations of the primary stem, the pedicel growing closely parallel to the primary stem.

Clytia paulensis is an epizooite of other hydroids; it has been recorded from *Obelia dichotoma* by Cornelius (1982), a close congener of *Obelia australis*. It also occurs on sponges in Port Phillip Bay, Victoria.

This is the second record of the species from Australia and the first from eastern Australia.

Genus Silicularia Meyen, 1834

Silicularia undulata (Mulder & Trebilcock, 1914)

Fig. 3A–F

Eucopella undulata Mulder & Trebilcock, 1914: 10, pl. 2, figs 5–7.

Silicularia undulata (Mulder & Trebilcock). – Bale, 1914: 87, 89; 1919: 327. – Blackburn, 1938: 324.

Material and records. NMV F51796 microslide. Whitfords Reef, Marmion, Western Australia, on *Amphibolis antarctica*, 3 m, J. E. Watson, April, 1986. NMV F51795 microslide Queenscliff, Victoria, on *Amphibolis antarctica*, 3 m, J. E. Watson, 21/1/1987.

Description. Hydrorhiza reticulating, flat and ribbon-like, with a wide stolonal canal and a delicate flange of perisarc at each side. Hydrothecal pedicels short, to 2 mm in height, thickest at junction with the hydrorhiza, otherwise of same diameter throughout. Pedicel terminating in a distal shoulder bearing a flattened spherule slightly narrower in diameter than pedicel. Perisarc of pedicel thick, deeply annulated throughout but sometimes with a short, smooth proximal section.

Hydrotheca bilaterally symmetrical, bowl-shaped, wider than deep (mean depth/width ratio 1:1.2), with a conspicuously thickened asymmetrical base, hydrothecal margin smooth, sloping obliquely to one side. Hydranth large, robust, with about 24 tentacles, too large to retract into the hydrotheca.

Colonies dioecious, gonothecae of both sexes large, irregularly circular to elongate oval, perisarc thick and slightly undulated, borne on a very short pedicel arising from the hydrorhiza, mature gonotheca flattened to the substrate. Aperture distal, subcircular, slightly depressed into the body, surrounded by a thickened rim and sealed by an operculum.

Mature female gonophore a large sporosac containing 15–20 ova with a smaller, developing gonophore below.

Measurements of *S. undulata* from Western Australia and Victoria are compared with those of *S. rosea* (author's collection) (Table 1).

Colour. White.

	Measurements (mm): *S. undulata* Range	Mean	*S. rosea* Range	Mean
Hydrorhiza				
Width	0.25–0.35	0.30	0.32–0.37	0.35
Pedicel				
Length	0.55–1.13	0.77	0.75–3.38	2.07
Distal width	0.09–0.13	0.10	0.12–0.22	0.20
Diam. of spherule	0.07–0.10	0.09	0.10–0.13	0.11
Hydrotheca				
Maximum depth	0.23–0.36	0.31	0.30–0.68	0.49
Maximum width	0.30–0.45	0.39	0.50–0.70	0.62
Gonotheca				
Length	1.03–1.50	1.23	1.80–1.90	1.82
Maximum width	1.13–1.58	1.29	0.75–1.35	1.05
Length of pedicel	0.08–0.13	0.10	0.20–0.30	0.25

Table 1. Comparison of dimensions of *Silicularia undulata* with *Silicularia rosea*. (N = 10)

Remarks. Silicularia undulata has been recorded from Victoria (Mulder & Trebilcock 1914) and from Spencer Gulf, South Australia (Blackburn 1938). Although Blackburn (1942), and Ralph (1956), cite New South Wales as a locality, there is no record of *S. undulata* ever having been found on the Australian east coast.

In their original description, Mulder & Trebilcock (1914), noted the association of the species with the seagrass '*Cymodocea zosterifolea*' [= *Amphibolis antarctica* (Labill.) Sonder et Aschers] and although Blackburn (1938) did not record a substrate at the Sir Joseph Banks Islands, his specimens probably also came from the extensive seagrass meadows at this locality.

Mulder & Trebilcock (1914) and Bale (1914, 1919), distinguished *Eucopella undulata* from the closely related *Eucopella campanularia* von Lendenfeld, 1883, by its annulated stems and decumbent gonothecae. *Eucopella campanularia* was considered by Ralph (1956), to be a temperate-water '*subtropica*' form of *Silicularia bilabiata* (Coughtrey, 1875) which was later synonymised in *Silicularia rosea* Meyen, 1834, by Millard (1968, 1971, 1977).

Study of material collected from the seagrass meadows of southern Australia shows that, while closely related to *S. rosea*, *S. undulata* is sufficiently different to warrant it being considered a distinct species. *Silicularia undulata* is a smaller species than *S. rosea*, the difference in size being constant over its geographic range. Its annulated stems and recumbent gonothecae further distinguish it from *S. rosea*.

In contrast to the open stolonal connections characteristic of the Campanulariidae, in *S. undu-*

lata each new stolon emergcs from its predecessor through an orifice in the hydrorhizal perisarc similar to the cmergencc of a new pedicel (Fig. 3C).

The colonies are sparingly fertile, usually bearing fewer than four gonothecae. The gonotheca commences growth as an irregular, fan-shaped or cornucopia-like bud from the hydrorhiza, later bending towards, and spreading on the seagrass leaf until at maturity it reclines upon a wide shelf of perisarc. Irregularitics in shape of the maturc gonothcca result from encountering obstructions during the prostratc stage of growth (Watson 1992).

Ralph (1956) and Harris (1990) showed that thc gonophore of *S. rosea* is eumcdusoid in structure. Examination of fresh matcrial of *S. undulata* suggests that the gonophore of this species may be

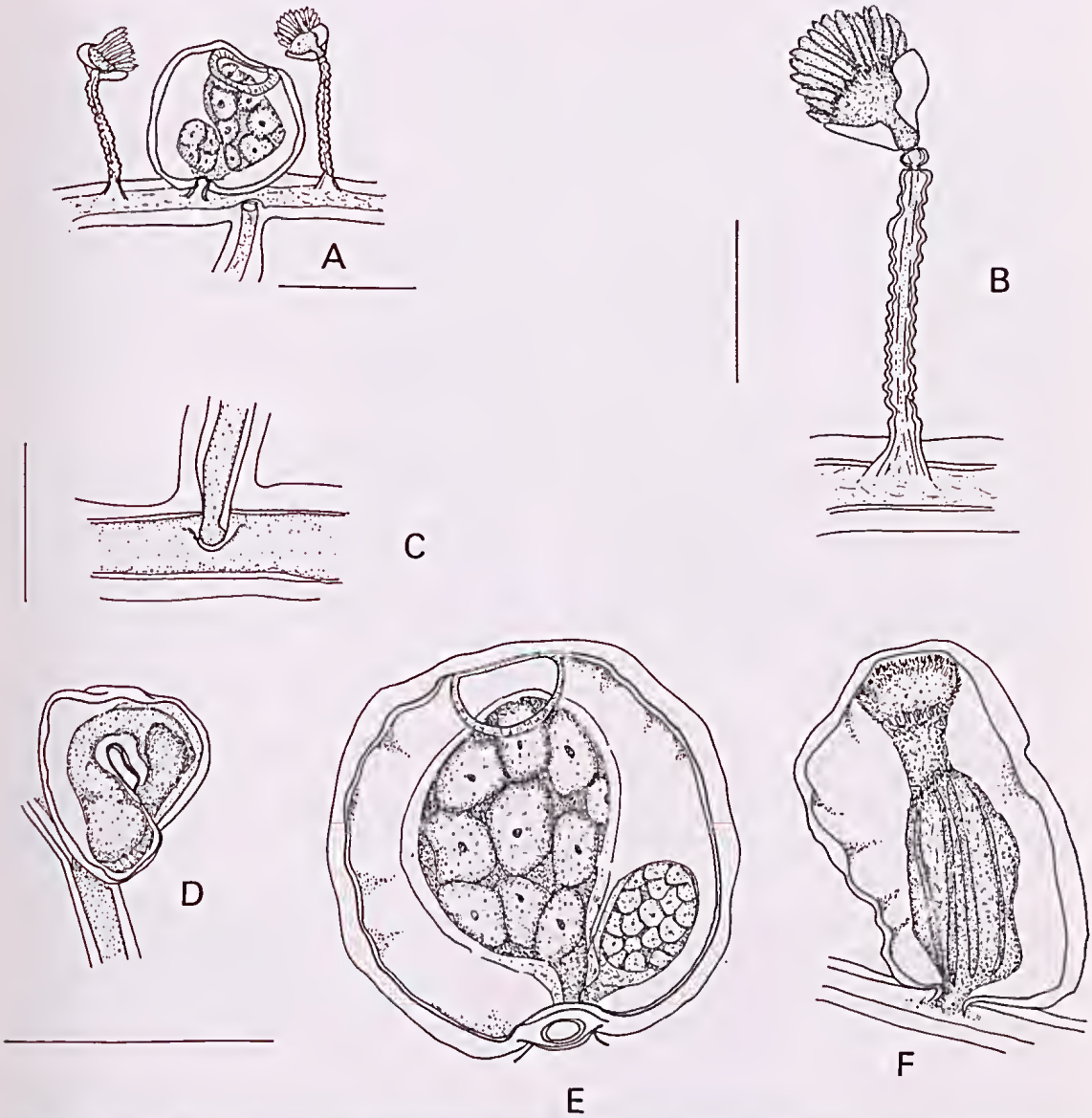

Fig. 3. A–F, *Silicularia undulata* from Marmion, Western Australia. A, part of female colony. B, hydrotheca fully retracted hydranth. C, hydrorhiza showing junction of stolonal canals. D, young gonotheca budding from hydrorhiza. E, mature female gonotheca with gonophore. F, mature male gonotheca with gonophore. Bar scales: A, D–F, 1 mm; B, C, 0.5 mm.

cryptomedusoid. It commences growth as a clearly recognisable hydranth which later degenerates, swelling to accommodate the sporosac while the aborted tentacles plug the aperture until release of the gametes.

An unusually large number of nematocysts of two kinds are always present in the hydrorhiza and hydrocaulus, a phenomenon also noted in some species of *Eudendrium* (Watson 1985). Both kinds of nematocysts are long and cigar-shaped, the larger being 15 μm long and 2–3 μm wide, and the smaller 6 × 1–2 μm. None were discharged.

Ecology and distribution. *Silicularia undulata* is a seagrass obligate endemic to Australia (Watson 1992). The weakly adherent hydrorhiza restricts the colonies to the most sheltered microhabitat in the axils of the seagrass leaves. Small colonies consisting of a few hydrocauli with short, robust stems, asymmetrical hydrothecae tilted to optimise water flow across the tentacles and gonothecae strongly recumbent to the substrate are adaptations necessary to survive the rigors of the seagrass habitat (Watson 1992).

Its congener, *S. rosea,* has southern circumpolar distribution (Ralph 1956). In southern Australia it is a common epiphyte of the brown algae *Scytothalia dorycarpa*, *Seirococcus axillaris* (R. Brown ex. Turner) Greville, *Ecklonia radiata* (C. Agardh) J. Aghardh and *Phyllospora comosa* (Labillardière). C. Agardh (see Shepherd & Watson 1970; Watson, unpubl.). *S. undulata* may be an example of speciation from the widespread parent *S. rosea* stock into the more specialised habitat of the seagrass meadow.

Family Thyroscyphidae Mammen, 1965

Genus Thyroscyphus Allman, 1877

Thyroscyphus macrocytharus (Lamouroux, 1824)

Fig. 4A, B

Lamouroux (1824) described *Clytia macrocythara* from material collected by the voyage of the *Uranie* and *Physicienne* to south-western Australia. Billard (1909) gave dimensions of the species held in the Lamouroux collection of l'Institut Botanique de Caen. Bale (1884) described *Campanularia marginata* from south-eastern Australia, distinguishing it from *Clytia macrocytharus* by its erect hydrocauli with three to four stem internodes, compared with the single stem internode of *Campanularia marginata*. The reproductive structures of neither species was then known.

Obelia marginata Allman, 1877, a similar but taller species with erect stems from the Atlantic, has been variously referred to *Campanularia* by Nutting (1915), to *Lytoscyphus* by Ritchie (1909) and Billard (1910), and to *Cnidoscyphus* by Splettstösser (1929). Recently, Calder (1983), assigned Allman's species to *Thyroscyphus* and renamed Bale's junior secondary homonym, *Thyroscyphus balei*. The finding of abundant fertile colonies with simple and compound stems in south-western Australia (Borowitzka et al. 1989; Watson 1992) now permits reappraisal of the status of Bale's and Lamouroux's species. I have examined a series of Bale's Canada Balsam mounted microslides of *Campanularia marginata* from Bondi Bay, New South Wales, and from Queenscliff and Portland, Victoria, held in the Museum of Victoria. The Victorian specimens (NMV F58791 and F58792) are considered by Stranks (1993) to be probable syntypes. Other than complexity of the hydrocaulus there are no morphological differences that distinguish *C. macrocythara* from *C. marginata*. *Thyroscyphus balei* (= *C. marginata*) is thus considered a synonym of *Thyroscyphus macrocytharus*.

Clytia macrocythara Lamouroux, 1824: 647, pl. 93, figs 4, 5.—Lamarck, 1837: 199.
Campanularia marginata Bale, 1884: 54, pl. 1, fig. 2; 1888: 758.—Bartlett, 1907: 62.—Levinsen, 1913: 289.
Laomedea marginata (Bale).—von Lendenfeld, 1885: 404.
Campanularia macrocythara (Lamouroux).—Billard, 1909: 311.
Thyroscyphus marginatus (Bale).—Bale, 1914: 91; 1915: 245, 258.—Stechow, 1924: 69; 1925: 217.—Blackburn, 1942: 112.—Watson, 1973: 169.—Harris, 1990: 232–260.
Thyroscyphus balei Calder, 1983: 16.—Watson, 1992: 220.
Non Thyroscyphus marginatus (Allman, 1877). (See Calder 1983: 16, 1991: 79, for synonymy.)

Material and records. NMV F51800, microslide. Whitfords Reef, Marmion, Western Australia, 4 m, on stems of *Amphibolis antarctica*, J. E. Watson, 30/1/1986.

Description. Colonies creeping, hydrorhiza tubular, undulating. Stems arising as an extension of the hydrorhiza, either simple with a single terminal hydrotheca or erect, and bearing up to six hydrothecae. Cauline internodes long and straight, perisarc usually undulating, sometimes smooth, widening to a distal apophysis. Hydrothecae on compound hydrocauli usually all facing the same side of stem, each borne on a very short, narrow pedicel from the stem apophysis. Hydrothecae very large, campanulate, expanding evenly from base to margin, the hydranth supported on a distinct, flattened shelf above base. Margin circular to

somewhat quadrangular, with heavily thickened rim, a deeply indented submarginal ring below margin and four equidistant low, blunt marginal teeth. A low opereulum of four equal triangular valves present in young hydrotheeae. Hydranth very large and robust with about 20 short, stubby tentaeles. Gonotheca borne on a short pedieel arising from the internode immediately below the hydrotheeal apophysis, barrel-shaped, often asymmetrical with one side more convex than the other, walls broadly undulating, maximum diameter just below mid-region, distal end truncated, summit

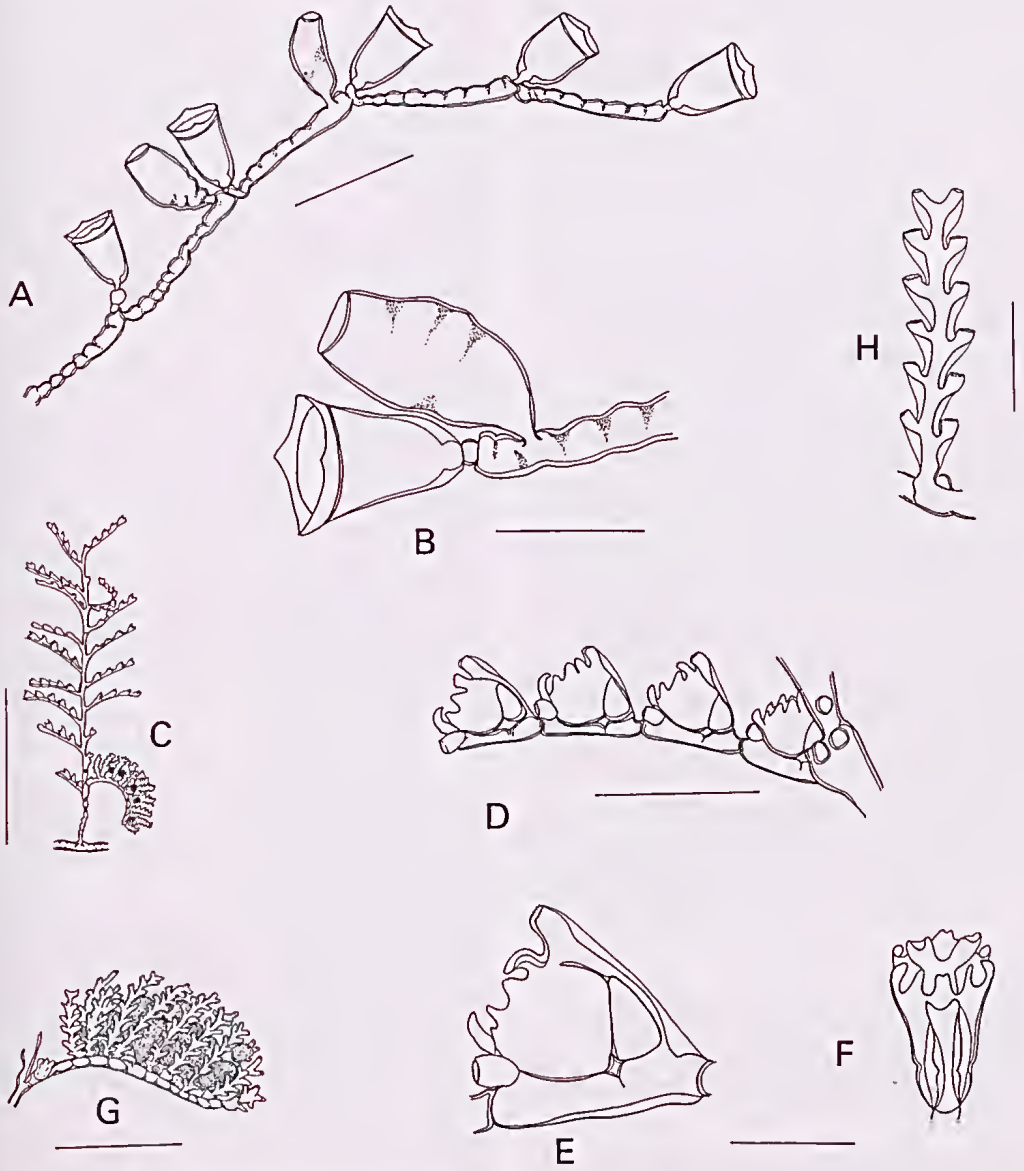

Fig. 4. A–H. A, B, *Thyroscyphus macrocyatharus* from Marmion, Western Australia. A, part of colony. B, hydrotheca and gonotheca from same colony, enlarged. C–F, *Aglaophenia postdentata* from Marmion, Western Australia. C, fertile stem. D, part of hydrocladium. E, hydrotheca, lateral view. F, hydrotheca, anterior view. G, corbula with mature gonophores. H, corbula rib. Bar scales: A, 2 mm; B, G, 1 mm; C, 4 mm; D, 0.5 mm; E, F, 0.2 mm.

often depressed, without aperture. Female gonophore a fixed sporosac containing two or three large ova surmounted by a plug of tissue. Male gonophore unknown.

Measurements (mm). Width of hydrorhiza 0.28–0.65, height of stems to 15, length of cauline internodes 1.90–2.75, width at distal apophysis 0.18–0.39, depth of hydrotheca from base to margin 1.05–1.35, diameter of basal shelf 0.37–0.59, height above base of hydrotheca 0.09–0.18, diameter at margin 0.53–0.57, submarginal ring 0.10–0.18 below margin, length of gonotheca 1.50–1.63, maximum diameter 0.80–0.81, width at summit 0.50–0.58.

Colour. Perisarc brown, hydranth often yellow; colony frequently overgrown by pink crustose coralline algae.

Remarks. The hydrotheca of *T. macrocytharus* is one of the largest Australian hydroids. The dimensions given by Billard (1909), for Lamouroux's type material indicate a shorter, but wider hydrotheca and shorter stem internodes.

In addition to the strongly developed floor supporting the hydranth, there is a second internal shelf in the hydrotheca about one third the distance up from the base. This shelf probably provides a supplementary anchorage for the very large and heavy hydranth. A detailed account of the physiology, adaptations and growth of *T. macrocytharus* (as *T. marginatus*) is given by Harris (1990).

The perisarc of the colonies is unusually thick throughout, imparting a woody brittleness to the hydrocauli and many show evidence of repeated breakage and regeneration. The species is very abundant on the stems of *Amphibolis* seagrasses in south-western Australia which habitat it shares with *Stereotheca elongata* (Lamouroux, 1816) (see Watson 1992).

The species is less common in cool temperate southern Australia where colonies are usually small and sterile (Watson 1973 and unpubl.). The deepest record of *T. macrocytharus* is from 137 m, off the coast of South Australia (Bale 1915). Stechow's (1925) record is from 3–14 m on algae, from Geraldton, Western Australia.

The finding of *T. macrocytharus* in the same region of Western Australia as its presumed type locality, confirms Lamarck's (1837) ecological note of 'Habite sur le *Zostera antarctica* sur les côtes de l'Australasie'.

Family Aglaopheniidae Broch, 1918

Genus Aglaophenia Lamouroux, 1812

Aglaophenia postdentata Billard, 1913

Fig. 4C–H

Aglaophenia postdentata Billard, 1913: 100, fig. 89.—Jäderholm, 1920: 8, pl. 2, fig. 8.—Vervoort, 1941: 231.—Redier, 1966: 97, pl. 3, fig. 4.—Millard & Bouillon, 1973: 90, fig. 11G, H.—Ryland & Gibbons, 1991: 557, fig. 24A–D.

Material and records. NMV F51799. Microslide, female colony, 6 km off Marmion, Perth, Western Australia, on *Thalassodendron pachyrhizum* leaves, 24 m, J. E. Watson, 30/1/1986.

Description. Hydrorhizal stolons long, straight and tubular, intersecting at regular intervals, sides flattened and extended into delicate flanges loosely adherent to the substrate, mature hydrorhiza with regular flexion joints (see below) extending into the stolon. Hydrocauli pinnate, unfasciculed and unbranched, proximal two or three internodes athecate, with thick perisarc and strong, oblique hinge joints, basal internode without nematothecae, the following one or two internodes each with a single nematotheca in the proximal third. Succeeding cauline internodes slender, perisarc thick, nodes usually an indistinct transverse constriction just above the hydrocladial apophysis. Hydrocladia alternate, given off from the apophyses on the front of the stem, short, usually with six short thecate internodes with distinct transverse joints. Hydrotheca small, occupying the entire internode, axis at an acute angle to the internode, posterior angular, adcauline wall flat to slightly convex, abcauline wall a smooth, convex curve, an intrathecal septum directed slightly backwards between the adcauline and abcauline walls. Margin with 10 apertural teeth: four paired lateral teeth and two, unpaired, one in the abcauline, and one in the adcauline median position. Abcauline median tooth almost rectangular in outline (anterior view), obscured in lateral view. First paired lateral teeth (abcauline view) leaf-shaped, margins outrolled, each tooth arched inwards over the hydrothecal aperture; second and third paired teeth broadly lobed with deep embayments between, the fourth pair shorter, lobe-shaped, situated behind the lateral nematothecae (difficult to see in lateral view), median adcauline tooth similar to median abcauline, but much longer and arched inwards over the aperture, edges rolled upwards. Median nematotheca closely adnate to the hydrotheca, distal end free from hydrotheca, abcauline wall straight, adcauline wall slightly swollen, canaliculate, with a ragged, truncate margin, the open side extending down to join the hydrotheca; a flange of perisarc connecting the distal end with the preceding hydrocladial node. Twin lateral nematothecae the same shape as cauline nematothecae, not extending past hydrotheca, one orifice circular, facing forward, with a second orifice into the

hydrotheca. Cauline nematothecae of same shape as the laterals, one on the proximal part of the internode and two side by side on the hydrocladial apophysis.

Colonies dioecious, corbulae numerous, usually borne in the proximal stem region but sometimes distal. Gonohydrocladium replacing a hydrocladium, arched backwards, with one proximal hydrothecate internode followed by six or seven, but sometimes up to 15 ribs. Gonohydrocladial internodes obliquc, distinct, each bearing a pair of corbula ribs with a single nematotheca at the base. Ribs free from base, arching over to meet at the top, with six or seven pairs of opposite to sub-opposite nematotheeae similar to laterals, apertures ragged and facing upwards, the outside of each pair connected to the inner side of the preceding pair by a thin flange of perisarc. Gonothecae small, lenticular, the female containing about six small ova.

Measurements (mm). Width of hydrorhiza including flanges 0.32–0.35, flexion joints extending 0.05 mm into stolon. Height of hydrocauli 10, length of proximal cauline internodes 0.75–1.13, succeeding internodes 0.30–0.45, width at nodes 0.06–0.08, length of hydrocladial internodes 0.28–0.35, width at nodes 0.04–0.05, length of hydrotheca posterior to marginal teeth 0.24–0.28, internal width at septum 0.10–0.12, maximum internal width 0.14–0.19, width at margin 0.16–0.19, length of unpaired adcauline marginal teeth (lateral view) 0.033–0.048, length of median nematotheca 0.31–0.35, length free from hydrotheca 0.04–0.06, width of adcauline side 0.04, width of terminal orifice 0.05; length of corbulae to 3, length of gonohydrocladium 0.70–0.75, width across rib 0.20–0.25.

Colour. Colonies yellow in life; gonophores pink.

Remarks. *Aglaophenia postdentata* was first recorded from Australia by Watson (1992), from *Amphibolis* seagrasses and *Thalassodendron pachyrhizum* den Hartog, near Perth, Western Australia.

The dark markings which penetrate the hydrorhizae of many species are highly developed in *A. postdentata*. Several authors (Ritchie 1911; Philbert 1935; Picard 1952; Ralph 1961) have speculated on these markings and Watson (1973) considered them to be a response to life on a flexible substrate. Detailed examination of these 'flexion joints' shows them to be small, hollow, roughly key-hole shaped structures that penetrate the hydrorhiza from its outer edge to the stolonal canal: such joints are an excellent adaptation to relieve mechanical stress and thus prevent fracture of the hydrorhiza.

The most characteristic feature of *A. postdentata* and the one used by Billard (1913) to distinguish it from *Aglaophenia pluma* (Linnaeus, 1758), is the very long median adcauline tooth of the hydrothecal margin. In the present material, this tooth is much longer than that figured by Billard (1913). The manner in which this, and the other apertural teeth arch over the hydrotheca, and the outrolled, leaf-shaped paired laterals, is diagnostic of the species. However, without careful examination from all angles these features are often very difficult to see.

New colonies commence growth from a small stolonal plate (Watson 1973) which spreads over the surface of the host, projecting a single stolon that matures into the hydrorhiza.

The hydrotheeae of *A. postdentata* are morphologically uniform, there being no increase in the length of the median hydrothecal nematotheca distally along the hydrocladium as occurs in some aglaophenian hydroids. The wide, ragged terminal orifices of the median and gonohydrocladial nematotheeae, which appear on casual inspection to be broken edges, are a constant and characteristic feature of *A. postdentata*.

Hydrocauli of *A. postdentata* from Australia are taller than those reported by Millard & Bouillon (1973) from the Seychelles. Since the corbulae of their material consisted of only two or three ribs compared with the six to 15 in the Australian specimens, it is likely that the Seychelles specimens were immature.

Aglaophenia postdentata is a tropical species previously recorded from north-western New Guinea and the Makassar Straits (Billard 1913), the Java Sea (Jäderholm 1920; Vervoort 1941) the Seychelles in the northern Indian Ocean (Millard & Bouillon 1973), and Fiji (Ryland & Gibbons 1991). The extension of the range of *A. postdenta* from the tropical Indo-Pacific to south-western Australia suggests larval transport southwards along the Western Australian coast by the Leeuwin current (Cresswell 1991).

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